

## **The effects of environmental warming on Odonata: a review**

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### **ABSTRACT**

Climate change brings with it unprecedented rates of increase in environmental temperature, which will have major consequences for the earth's flora and fauna. The Odonata represent a taxon that has many strong links to this abiotic factor due to its tropical evolutionary history and adaptations to temperate climates. Temperature is known to affect odonate physiology including life-history traits such as developmental rate, phenology and seasonal regulation as well as immune function and the production of pigment for thermoregulation. A range of behaviours are likely to be affected which will, in turn, influence other parts of the aquatic ecosystem, primarily through trophic interactions. Temperature may influence changes in geographical distributions, through a shifting of species' fundamental niches, changes in the distribution of suitable habitat and variation in the dispersal ability of species. Finally, such a rapid change in the environment results in a strong selective pressure towards adaptation to cope and the inevitable loss of some populations and, potentially, species. Where data are lacking for odonates, studies on other invertebrate groups will be considered. Finally, directions for research are suggested, particularly laboratory studies that investigate underlying causes of climate-driven macroecological patterns.

### **INTRODUCTION**

The causes of the current phase of environmental warming have received a great deal of attention both from within the scientific literature and in the public sphere. The main driver behind contemporary warming is now considered to be anthropogenic, mainly because of the unprecedented rate of increase in temperature (Karl & Trenberth 2003; Mann 2007). However, regardless of the causes of these variations in temperature, the current state of climatic flux provides an important opportunity to conduct natural experiments into the impacts of varying temperature on the world's biota.

Quaternary studies have shown using climate proxies that flora and fauna have survived rapid climate fluctuations in the past (Coope 1995a, b; Adams et al. 1999;

Davis & Shaw 2001). It has been reasoned that, since all extant species must have had progenitors who survived those past fluctuations, all extant species must possess adaptations that would enable them to cope with the same hurdles again (Balmford 1996). This is supported by the range of biological responses that have been documented (Parmesan 2006).

The Odonata have a long history in the fossil record relative to other orders, with fossils present from the Lower Permian (Wootton 1981). This fact, coupled with a range of adaptations which have enabled them to colonise temperate and subarctic habitats from their tropical origins (Pritchard & Leggott 1987), make them ideally suited to surviving current climate change. This review will consider the impact of environmental warming on a range of aspects of odonate biology to investigate how true this intuitive assumption may be.

A variety of factors make the Odonata an ideal model taxon for the investigation of the impacts of environmental warming and climate change. These include:

(1) a tropical evolutionary origin potentially leading to limitations of distribution by temperature; (2) the use of temperature in seasonal regulation; (3) high local abundances in some species, making fieldwork involving ecological sampling not only feasible but relatively straightforward; (4) a long history of scientific research, into both their ecology and behaviour; (5) extensive amateur recording, resulting in large historical databases of sightings.

This review is arranged hierarchically according to levels of organisation, beginning with physiological impacts of temperature on life-history parameters and thermoregulation. Then species interactions within habitats are discussed before moving onto the distributions of Odonata and their habitats in the landscape. Finally, the influence of temperature on broader topics such as evolution and extinction risk is considered.

## LIFE HISTORIES

### Development

The intuitive link between increasing temperature and increasing developmental rate has been illustrated in a range of laboratory experiments in larvae (Pickup & Thompson 1990; Krishnaraj & Pritchard 1995; Pritchard et al. 2000; Van Doorslaer & Stoks 2005) and in the egg stage (Masseau & Pilon 1982). The Odonata are unique in being the only taxon of aquatic insects which exhibits solely negative relationships between egg development time and temperature (Pritchard et al. 1996). The population model developed by Crowley et al. (1987) considered a direct effect of temperature on development rate only in the egg stage, with indirect effects of temperature via feeding rates in 'small' and 'large' larval classes (as demonstrated by Lawton et al. 1980). Subsequent work has not only supported this indirect effect, but also illustrated that a direct effect is also present (Van Doorslaer & Stoks 2005).

Population-level adaptations in developmental rate to local thermal regimes have been demonstrated in *Argia vivida* Hagen in Selys, a species found in a range of temperature environments (Leggott & Pritchard 1985). This adaptation needs to be borne in mind otherwise predictions of future growth rates under environmental warming will underestimate true values. A range of studies have pointed to high thermal thresholds for development compared to other invertebrates, both in the egg

(11.25°C *Argia vivida*, Leggott & Pritchard 1985; 12°C *Coenagrion puella* [Linnaeus], Waringer & Humpesch 1984) and larvae (8°C *Ischnura elegans* [Vander Linden], Thompson 1978c). Species-level adaptation to varying hydroperiod has been proposed as a mechanism by which growth rate has been accelerated in *Lestes* spp. (De Block et al. 2008a). This is particularly pronounced in *L. dryas* Kirby, which inhabits vernal pools (with annual drying).

### Temperature and photoperiod

Responses to temperature in nature are potentially complicated by a range of species-specific responses to changing photoperiod (summarised in Corbet 1999: 288). Photoperiodic cues are thought to play a role in regulating larval development (Norling 1984b) and, as such, influence the temperature-developmental rate relationships described above. In order to properly consider the effects of either variable, the other needs to be accounted for.

The effect was first observed in *Anax imperator* Leach (Corbet 1955, 1956a) and early experiments showed that a longer photoperiod accelerated development on *Tetragoneuria cynosura* (Say) (Jenner 1958; Lutz & Jenner 1960; Lutz 1963). The same experimental paradigm has been used in many studies to examine effects of temperature and photoperiod (Sawchyn & Church 1973; Corbet et al. 1989). However, it was not until a tightly controlled experiment by Johansson & Rowe (1999) on *Lestes congener* Hagen that an increase in developmental rate (moult frequency) was unequivocally demonstrated. However, such an increase in developmental rate was not mirrored by an increase in growth rate, a finding confirmed in a study on *Lestes viridis* (Vander Linden) (De Block & Stoks 2003). Both studies showed large effects of photoperiod on size and age at emergence.

Critical photoperiods – the light : dark ratio required to elicit a response such as diapause – have been shown to vary with latitude in a range of insects (Danilevskii 1965), as well as in odonates (Norling 1984a). This variation has also been shown in *Aquarius paludum* (Heteroptera: Gerridae), to occur over time at the same location, with the suggestion that increasing environmental temperature may be the cause (Harada et al. 2005).

In addition to a photoperiodic modulation of temperature-development relationships, low temperatures can also influence photoperiodic responses. *Enallagma hageni* (Walsh), a northern species, was shown to exhibit photoperiodic responses at lower temperature than *Enallagma aspersum* (Hagen), a southern species (Ingram & Jenner 1976).

### Diapause

The high incidence of diapause in Odonata compared to other taxa has been taken as evidence for a tropical origin and invasion of temperate regions (Pritchard & Leggott 1987). Diapause induction and cessation have been shown to be elicited by photoperiod and temperature in a range of odonates (Corbet 1956b; Boehms 1971; Sawchyn & Church 1973; Ingram 1975; Corbet et al. 1989; Pritchard 1989). These studies provide good evidence for Norling's (1984b) two-stage model of diapause induction. The evolution of diapause as a mechanism for colonising temperate regions from the tropics has been implicated in speciation processes in American taxa (Pritchard 2008).

The reliance of diapause on low temperatures may place some species at risk if certain temperature thresholds are passed during environmental warming. Diapause induction avoids periods of low energy availability for ectotherms and low food availability. If diapause induction fails due to high temperatures, developmentally active ectotherms may suffer increased mortality (Harrington et al. 2001). Current development models do not include temperature as a factor affecting diapause (Braune et al. 2008).

## Phenology

The study of phenology has received rigorous attention in the past decade and has shed much light on the responses of invertebrates (Roy & Sparks 2000), vertebrates (Crick & Sparks 1999) and plants (Fitter & Fitter 2002) to changing temperatures. A recent meta-analysis of a range of taxa (thought not including Odonata) gave an estimate of advancement in spring phenology of  $2.8 \text{ days} \cdot \text{decade}^{-1}$  (Parmesan 2007). British Odonata follow the same pattern in response to warming, with the flight periods beginning progressively earlier in the year (Hassall et al. 2007). Hassall et al. demonstrate that the odonate phenological response is species specific, being modulated by the presence of a diapause stage in the egg. While the leading edge of the flight period advanced, the trailing edge exhibited a range of responses between tracking of the leading edge and regressing to later in the year.

Subsequent analyses of more detailed, though briefer, time series have suggested that different temperature variables have different effects on phenology (Dingemanse & Kalkman 2008). At still higher resolution, Richter et al. (2008) produced a temperature-sum model to describe the emergence of *Gomphus vulgatissimus* (Linnaeus), which performed well when checked using field data. These three studies offer strong support for the role of temperature in determining phenology.

Patterns of emergence vary spatially and temporally between species. In addition to the distinction between spring and summer species (Corbet 1954), particular species may exhibit multiple peaks in emergence. In some cases this may be due to simple bi- or multivoltinism. Alternatively, an overlap of generations within a population close to a voltinism threshold can result in cohorts exhibiting different voltinisms emerging at different times during the same year (see the appendix of Corbet et al. 2006 for a thorough review). Models have predicted that species will increase substantially the rate at which generations are produced (Braune et al. 2008).

However, multiple emergence peaks also occur in species with a single voltinism class. An example is *Pyrrhosoma nymphula* (Sulzer) in northern Scotland (Corbet & Harvey 1989), which exhibits two peaks in emergence within a semivoltine life cycle due to larvae overwintering in one of two instars. While there are multiple explanations for variations in growth rate, temperature is often an important factor and increases in temperature would be expected to synchronise this emergence pattern into a single peak while potentially turning synchronised emergence events into multiple peaks.

Studies into the ecological impacts of changing phenology have shown that decoupling of trophic interactions is possible (Harrington et al. 1999; Walther et al. 2002; Winder & Schindler 2004). Such decoupling has been reported for birds feeding on larval Lepidoptera (Both & Visser 2005) and *Daphnia* grazing on diatoms

(Winder & Schindler 2004). It is often assumed that odonates are generalist predators and so phenological mismatching will not directly affect their trophic interactions. However, brief peaks in the abundance of prey species may provide a vital source of food when a high rate of food intake is required, e.g. during the early pre-reproductive period. Small odonate larvae are reliant on a relatively small range of prey due to limitations on the size of prey that can be captured (Thompson 1978b) resulting in a potential reliance on particular species.

Climate-induced variations in tipulid emergence on blanket bogs (which can form important odonate habitat) have been linked to the population dynamics of *Pluvialis apricaria*, a moorland wading bird (Pearce-Higgins et al. 2005). It might be expected that prey diversity would be low at higher latitudes and altitudes and that this would necessitate higher interaction strengths between the few remaining species in food webs. It would be worthwhile to investigate the diets of odonates at low prey diversities to establish whether such reliance (and, therefore, a risk of trophic decoupling) is present.

## THERMOREGULATION

Thermoregulation and the temperature biology of odonates has received extensive coverage elsewhere (May 1976, 1991). As a result, we shall briefly summarise the research on the different areas of thermoregulation.

### Pigmentation

Physiological colour change is a common feature of thermoregulation in Odonata (Corbet 1980) and is unusually common in Odonata compared to other taxa in central Europe (Sternberg 1996). It has been suggested that populations of some species vary in colouration with latitude to enhance the absorbance of heat in cooler regions, e.g. *Orthetrum cancellatum* (Linnaeus) (Hilfert-Rüppell 1998). As well as varying with latitude, pigmentation can also vary with temperature throughout the day, e.g. *Argia vivida* (Conrad & Pritchard 1989); *Aeshna caerulea* (Ström) (Sternberg 1996). This hypothesis is supported further by the observation that the abdomen of *Ischnura elegans*, which is active at relatively low temperatures, is 90% black compared to 40% for *Coenagrion puella* and *Enallagma cyathigerum* (Charpentier), which are not active at lower temperatures (Hilfert-Rüppell 1998). Such a pattern could be investigated more thoroughly using modern spectroscopic techniques.

Although the indirect evidence was not at first supported by experimental work (e.g. Veron 1974), Sternberg (1989, 1990) showed that there was an appreciable impact of colouration on body temperature in some Anisoptera. Evidence for a communicative function for body colouration has been equivocal at best whereas a thermoregulatory role for melanistic forms has been shown in other taxa (Sternberg 1996). In a carefully controlled experiment Sternberg (1996) showed conclusively that colour phase impacted on the rate of heat gain. He measured the rate of warming in different colour phases exposed to the same source of radiant energy as well as comparing the amount of time taken to reach thermal limits for behaviours, viz. eye-cleaning, wing-whirring and take-off, during warming.

Sternberg (1996) proposed that the higher frequency of androchrome females at lower latitudes may be due to the need for greater thermoregulation. He also speculated that this form of thermoregulation partly contributes to the difference between the bimodal diel activity patterns of *Aeshna* females which cannot thermoregulate through colour change and the unimodal diel activity patterns of *Aeshna* males that are capable of colour change.

### Basking

The use of solar radiation in thermoregulation has been documented extensively in odonates in the field (e.g. Hilfert-Rüppell 1998). Laboratory experiments have also confirmed the effectiveness of 'obelisking' (May 1976) in reducing heat absorption. Field experiments have shown that *Aeshna caerulea* can use its wings to effectively increase body temperature by creating a 'glasshouse' (Sternberg 1990).

### Microhabitat use

Although habitat requirements of Odonata are relatively poorly understood, there is strong evidence for selection of warmer pools (with high humic content, shallowness and a dark benthos) as oviposition sites in the boreal *A. caerulea* (Sternberg 1997). The colonisation of North America by the genus *Argia* has been attributed to a selective use of geothermally heated streams (Pritchard 1982). Given the propen-

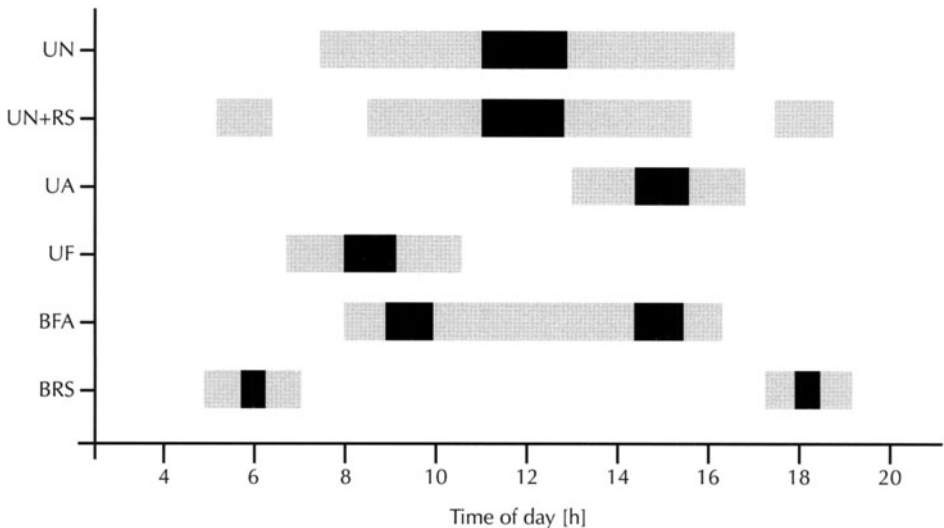


Figure 1: Proposed diel patterns of adult activity in Odonata; redrawn from Corbet (1999: 304). Grey bars indicate active periods and black regions are peaks in activity. UN: unimodal noon; UN+RS: unimodal noon plus sunrise and sunset; UA: unimodal afternoon; UF: unimodal forenoon; BFA: bimodal forenoon and afternoon; BRS: bimodal sunrise and sunset.

sity of Odonata to inhabit microhabitats with warmer thermal regimes, a greater understanding of microhabitat occupancy and the variation in the varying thermal regimes within water bodies is vital if we are to predict impacts of atmospheric warming. Adults of *Lestes sponsa* (Hansemann) have been shown to exhibit body temperatures significantly higher than ambient temperature by perching in sunflecks (Watanabe & Taguchi 1993). These sylvan damselflies were also able to utilise forced convection, the importance of which has been demonstrated experimentally in *Anax junius* (Drury) (May 1976), to reduce heat gain in sunflecks that were too warm. Anisoptera inhabiting deserts have been shown to exhibit substantially higher thoracic temperatures and thresholds for flight than congeners and conspecifics from cooler habitats, suggesting that a degree of adaptation to extreme thermal environments may be possible (Polcyn 1994).

### Activity patterns

As well as varying spatial patterns of activity, the temperate zone provides a broad thermal niche which can be exploited by varying temporal activity patterns. Corbet (1999: 303) defines six discrete diel patterns of activity (DAP, see Fig. 1) which rank along a continuum of thermal requirements from unimodal (UN – characteristic of odonates in temperate environments) to bimodal with activity only at sunrise and sunset (BRS – characteristic of some odonates in tropical environments). It might be expected that species would vary activity patterns across their ranges and, as the environment warms, over time at a single site.

### Wing-whirring

In addition to the above mechanisms for thermoregulation, odonates also exhibit thermoregulatory behaviours more commonly seen in endotherms. In particular, a number of species perform 'wing-whirring', which enables a build up of metabolic heat originating in the flight muscles. At least one member of each American family of Anisoptera is capable of such behaviour and this can lead to warm-up rates of between 0.9 and 6.7°C·sec<sup>-1</sup> (May 1976). Regulation of body temperature is also performed through controlling circulation of haemolymph through the thorax and abdomen (for a review of these topics, see May 1976). However, some species are so adapted to their boreal habitat that they exhibit upper thermal thresholds for flight, e.g. *Ischnura elegans* (Hilfert-Rüppell 1998); *A. caerulea* (Sternberg 1997).

## ECOLOGY

### Trophic interactions

Temperature has been implicated in determining the structure of aquatic communities (Carpenter et al. 1992; Heino 2002; Burgmer et al. 2007). Latitudinal patterns in species richness have been documented for a number of taxa, including Odonata (Eversham & Cooper 1998). As the climate warms, new communities will be formed as species shift their ranges at different rates (Hickling et al. 2006). Due to the sheer number of ecological interactions, it is impossible to consider all the implications of

such community shifts. Mesocosm experiments have suggested that a 3°C increase in water temperature would have negligible impacts on the structure of aquatic macroinvertebrate communities (Feuchtmayr et al. 2007), although natural odonate communities appear to exhibit high rates of turnover in response to changing climate (Flenner & Sahlén 2008).

However, one change which may occur – with serious repercussions for the aquatic community – is the progressive extinction of fish populations (Xenopoulos et al. 2005; Xenopoulos & Lodge 2006) coupled with the relatively low rate of colonisation in fish. While increases in the proportion of southerly distributed and warm water species have been reported in French rivers (Daufresne & Boët 2007), islands such as the UK and Ireland can receive no such colonisation apart from by artificial means.

In ecosystems in which they are present, fish dominate the rest of the food web by top-down pressure. However, fish also suppress large macroinvertebrate populations (Dorn 2008) including Odonata (Henrickson 1988; Bendell & McNicol 1995; Feuchtmayr et al. 2007) and fish predation affects the size of macroinvertebrates (Blumenshine et al. 2000). As fish populations become extinct, there is the potential for odonates to assume the role of top predator. Certainly, any change in the dominant predator will have substantial (and potentially unpredictable) impacts on prey communities (Soluk 1993). However, a brief comparison between the common fish *Gasterosteus aculeatus* (Hynes 1950) and detailed studies of *Ischnura elegans* (Thompson 1978a) and *Cordulegaster boltonii* (Donovan) (Woodward & Hildrew 2001) reveals a range of similarities in size and diet. The difference between fish and odonate predation certainly merits further research. Predation by fish on odonate larvae has also been linked to plant recruitment via the predation by adult odonates on pollinating insects (Knight et al. 2005). This highlights not only the complexity of natural systems but also the importance of considering the landscape and its constituent biotopes holistically.

The effects of varying temperature on the functional response of odonate larvae have been studied extensively in a number of species (Thompson 1978c; Gresens et al. 1982). Higher temperatures result in an increase in the asymptotes of the type II functional response in *I. elegans*. This was manifested in an increase in the attack coefficient and a decrease in handling time at higher temperatures (Thompson 1978c). The increased feeding rates at higher temperatures have also been linked to an increase in the rate of gut clearance at higher temperatures (Gresens et al. 1982). Clearly an increase in feeding rate in a top predator in aquatic ecosystems (e.g. *C. boltonii*, Woodward & Hildrew 2001) will have knock-on effects at other trophic levels.

Attempts to model the population dynamics of *I. elegans* (Crowley et al. 1987) have assumed a homogeneous prey population whose growth rate is related to temperature. However, the diversity of prey species available to a generalist such as an odonate and, therefore, the diversity of thermal responses is noted. As mentioned above, a further complication may arise through phenological decoupling of trophic interactions (Winder & Schindler 2004). Trophic cascades resulting from such events could influence higher trophic levels including the Odonata.



## Body size

Body size is potentially the most important parameter when considering an organism's ecology. It is also tightly linked to temperature, with larger body sizes at lower temperatures being reported in the majority of studies (for a review see Atkinson 1994). Body size in Odonata has been shown to affect to diet breadth (Thompson 1978b), handling time (Thompson 1978c) and rate of consumption (Woodward & Hildrew 2002). However, patterns in odonate body size have been under-studied.

The only attempt to quantify latitudinal variation in body size in Odonata was carried out by Johansson (2003). This study suggested a U-shaped relationship across the full extent of the geographical range, which has been tentatively explained using Bergmann and counter-Bergmann clines (Blanckenhorn & Demont 2004). There is evidence that such a U-shape may have a genetic basis (De Block et al. 2008b).

## Immunology

The effects of climate on invertebrate immunology has received relatively little attention, despite odonates having been studied extensively in the field and in the lab (Siva-Jothy 1999, 2000; Rantala et al. 2000; Rolff 2001; Yourth et al. 2002; Robb & Forbes 2005, 2006). Only one study has considered the impact of temperature on odonate immunity, in the context of variation in immune function across the flight season (Robb & Forbes 2005). This study clearly showed increased resistance to *Arrenurus planus* (Arachnidae) at higher temperatures, which results from higher haemocyte counts at higher temperatures (Pandey et al. 2007).

The implications for this temperature-mediated immunity lie in the determination of range margins. At a certain threshold of immune function, the immune challenge presented by the pathogen community may be result in too great a mortality. This would lead to the kind of small, unstable marginal populations that are found in nature (Brown 1984).

## Distributions

A great deal of work has been carried out to detect changes in the distributions of flora and fauna in response to climate change (Parmesan et al. 1999; Hickling et al. 2006; Hitch & Leberg 2007). However, before considering the implications of shifts in response to the current phase of warming, a context needs to be sought for these trends. This is provided by the literature on Quaternary climate change and associated shifts in distribution.

Quaternary climatic changes have been shown to be sudden and unpredictable (Adams et al. 1999). However, despite this insect populations appear to have survived with relatively little extinction (Coope 1995b). It has been suggested that the morphological stasis exhibited by the insect fossil record through the quaternary is indicative of a high degree of dispersal which compensated for shifting fundamental niches (Coope 1978). As mentioned above, the fact that extant taxa such as the Odonata possess a progenitor that has survived such rapid climatic transitions suggests that it has inherited a mechanism for surviving such challenges should they present themselves again (Balmford 1996). However, contemporary rates of climate change are substantially greater than previously experienced and anthropogenic disturbance constitutes an entirely novel extinction threat.

Understanding how odonate ranges have responded to changing climate and predicting how these responses will be manifest in the future requires knowledge of the mechanisms that determine the realised niche. Although temperature has been supported as a potential factor, there are other candidates which may at least contribute and the traits on which temperature acts are not clear.

An alternative climatic range determinant may be weather. Weather, and specifically the pattern of suitable oviposition days (Thompson 1990), has been implicated in affecting fecundity of populations. Precipitation and cloud cover patterns follow approximately the same geographical distribution as isotherms, with higher cloud cover and precipitation at higher latitudes where temperatures are lower. Thus multiple climatic variables may work synergistically to restrict odonate populations at range margins.

Low temperature may also increase stress during development (Chang et al. 2007). Zygopteran wings have been shown to be uniform in shape along a latitudinal gradient until close to the range margin where populations exhibit wings that become progressively further from the 'normal' shape (Hassall et al. 2008). It may be that this deviation from the norm is also a deviation from the most effective wing shape, leading to a decline in the fitness of populations exhibiting such deviations.

Contemporary shifts in the distributions of Odonata have been reported where good historical data have been available (Ott 1996, 2001, 2007; Aoki 1997; Hickling et al. 2006; Flenner & Sahlén 2008). Hickling et al. (2005) demonstrated a mean poleward shift in distributions of 74 km over 36 years between 1960 and 1995, or an annual shift of 2.1 km. This approximately corresponds to the upper limits of dispersal ability in extensively studied Zygoptera (Conrad et al. 1999; Angelibert & Giani 2003; Watts et al. 2004) and to the rates of range expansion predicted from temperature models of *Gomphus vulgatissimus* (Braune et al. 2008). A substantially higher rate of expansion has been recorded in Swedish species (Flenner & Sahlén 2008).

These results suggest that, given the appropriate habitat into which they may disperse, even the weaker-flying odonates, e.g. *Coenagrion mercuriale* (Charpentier), are capable of tracking changes in climate space. However, such a permeable habitat patch network is not guaranteed. Some regions contain high densities of lentic water bodies (Boothby & Hull 1997), but future predictions suggest that the characteristics and distribution of water bodies may vary with changing climate (Carpenter et al. 1992; Hostetler & Small 1999; Dawson et al. 2003). Climate-induced changes have also been predicted for lotic water systems (Pilgrim et al. 1998; Alcamo et al. 2003; Zwolsman & van Bokhoven 2007) and some studies have attempted to predict how these changes might affect stream communities (Xenopoulos & Lodge 2006).

## HABITAT

### Drought

Some studies have investigated tolerance to drought in macroinvertebrates, including odonates. Studies examining recolonisation following drought events have shown that aquatic macroinvertebrates can rapidly return to former habitats following refilling (Van De Meutter et al. 2006). The removal of fish and subsequent lag in recolonisation relative to macroinvertebrates was suggested as a reason for the increase in diversity following refilling (Van De Meutter et al. 2006; Dorn 2008). As men-

tioned above, fish are a major predator of Odonata and this may contribute to an expansion of odonate ranges. It should be noted, however, that some fish species also possess adaptations to drought, e.g. *Carassius carassius* (Piironen & Holopainen 1986).

The transition from permanent to temporary (both intermittent and episodic) water bodies that is predicted to occur in some cases (Carpenter et al. 1992) will affect different species in different ways. The selective pressures that temporary water bodies exert on fauna are quite different to those in permanent water bodies (Williams 1997). Some odonates possess adaptations that permit survival in seasonal ponds such as drought-resistant eggs, e.g. *Lestes* spp. (De Block et al. 2008a), drought resistant larvae, e.g. *Coenagrion hastulatum* (Charpentier) (Valtonen 1986), and rapid larval development, e.g. *Lestes sponsa* (Pickup & Thompson 1990). *Ischnura pumilio* (Charpentier) also exhibits a drought-resistant egg (Cham 1992) and this may aid in a recovery for the species if competitors are excluded by fluctuating water levels. Dragonfly assemblages inhabiting temporary wetlands in African desert and semi-desert areas differ from assemblages of non-desert areas and their constituent species tend to be highly mobile and multivoltine (Suhling et al. 2003).

Desiccation is a primary cause of egg mortality (Corbet 1999: 60) and so for species lacking such adaptations, reduced water permanence will reduce recruitment. This constitutes a substantial selective pressure towards the evolution of life-history traits that promote survival in more ephemeral water bodies, as has been seen in *Lestes* spp. (De Block et al. 2008a) and some species of Namibian Libellulidae (Suhling et al. 2005).

## Pollution

Increases in temperature bring increases in evaporation from water bodies with concomitant increases in the concentrations of pollutants (Carpenter et al. 1992). Odonates have been shown to be sensitive to pollutants (Clark & Samways 1996) and may suffer more than other taxa. Potential shifts in the trophic state of ponds and lakes due to warming (see Mooij et al. 2005 for a review) may also affect odonate persistence (Menetrey et al. 2005) as well as the macrophytes on which they rely for refuges (Thompson 1987).

## Landscape connectivity

A reduction in the number of habitable ponds will lead to a decline in the connectivity of the landscape. A range of modelling studies has attempted to calculate the impact of varying degrees of patch loss on landscape permeability (Collingham & Huntley 2000; Travis 2003; Opdam & Wascher 2004). However, in order to assess the impact of habitat fragmentation on odonates, two factors must be considered.

Firstly, the habitat must be carefully defined. Many species exhibit idiosyncratic requirements of their environment which can render even the densest freshwater landscape unsuitable. *Sympetrum danae* (Sulzer) epitomises this problem. A study of 1,000 ponds in the north of England showed that none of the 11 *Sphagnum* species recorded occurred in more than 52 of the ponds (Boothby 2000). The close association of *S. danae* with *Sphagnum* (Michiels & Dhondt 1990) is likely what resulted in the species only being found in nine out of 1,000 ponds, despite being widespread in Britain (Merritt et al. 1996).

Secondly, dispersal ability first needs to be quantified. Although a range of such studies exist (Hunger & Röske 2001; Purse et al. 2003; Watts et al. 2004), these are ultimately limited in the results that they can produce by resources (Slatkin 1985). Indeed, there appears to be a correlation between the size of the area surveyed in these studies and the amount of dispersal recorded (Fig. 2) like that found for butterfly dispersal studies (Schneider 2003).

In an extreme case of low landscape connectivity, insular populations of *Ischnura hastata* (Say) found on the Azores now exhibit uniform parthenogenesis (Cordero Rivera et al. 2005). It is possible that there are also parthenogenetic populations of other species on other islands (Sherratt & Beatty 2005).

### Sea-level rise

Another factor affecting habitat availability for Odonata may be predicted rises in sea levels (Meehl et al. 2005) and increasing frequency and severity of flood-causing precipitation events (Dale 2005) that accompany global warming. This pattern is predicted to lead to the loss of up to 22% of coastal wetlands globally by 2080 (Nicholls et al. 1999), although the extent may be greatly influenced by anthropogenic factors (Nicholls 2004). The flooding that threatens much of the coastline of south east England (Shennan 1993) has caused the extinction of *Coenagrion scitulum* (Rambur) in the UK (Hammond 1997) and threatens the fenlands that represent a stronghold for many species including the endangered *Aeshna isoeles* (Müller). However, there has been little work done on the regional threats of inland freshwaters to sea-level rise. Although there are some odonates which are tolerant of brackish water (e.g. *Lestes dryas*), inundation of sites could lead to destruction of invertebrate communities and associated plant communities.

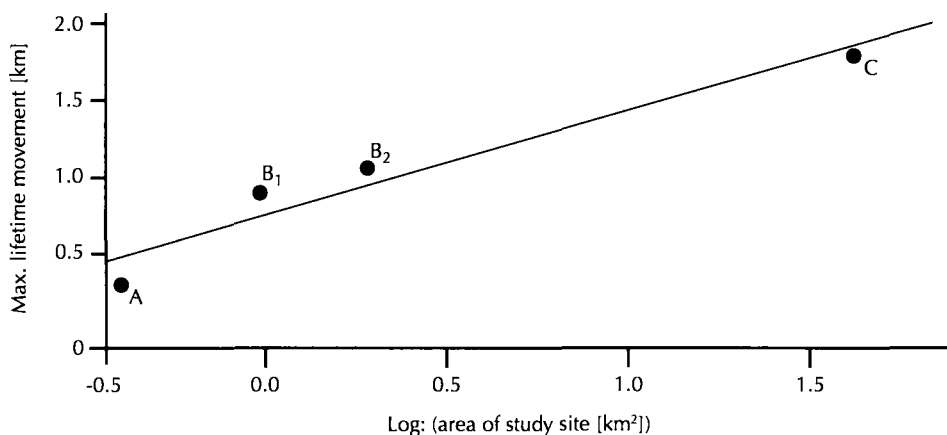


Figure 2: Relationship between the area of a study site and the maximum dispersal distance detected in four studies of *Coenagrion mercuriale* ( $r = 0.966$ ;  $p = 0.034$ ). A: Hunger & Röske (2001); B<sub>1</sub>: Purse et al. (2003) – New Forest site; B<sub>2</sub>: Purse et al. (2003) – Preseli site; C: Rouquette & Thompson (2007).

## EVOLUTION

### Adaptation

The Odonata have a long evolutionary history over which relatively little phenotypic change has occurred. However, adaptations which likely have a thermal basis have occurred in a range of species. *Aeshna caerulea* is a boreal species which has developed both unusual basking behaviour and physiological colour change to cope with the severe climate (Sternberg 1997). *Lestes* spp., on the other hand, have developed increased growth rates and drought-tolerant eggs to take advantage of ephemeral water bodies (De Block et al. 2008a). However, no within-species adaptation towards earlier egg hatching was found between populations of *L. viridis* inhabiting permanent and temporary water bodies (De Block et al. 2005).

On the other hand, within-species regional variations in growth rate (Leggott & Pritchard 1985; Pritchard 1989) and responses to seasonal cues for development (Norling 1984c) have been demonstrated. The selective basis and costs of adaptive developmental rates are clearly laid out by Arendt (1997). This may be a profitable avenue for research given the observed shifts in critical photoperiod in *Aquarius paludum* (Harada et al. 2005). However, no unequivocal adaptation during the current phase of climate warming has been documented.

### Processes at range margins

As climate space expands, it is intuitive to suppose that new habitats will be colonised by a non-representative sample of genotypes from the potential source populations. It has been proposed that populations at 'marginal' sites may possess exaggerated dispersal traits compared to those in 'core' sites because of the propensity for more highly dispersing individuals to found populations at the expanding range margin (Simberloff 1981). Examples include an increase in the proportion of macropterous (dispersing) individuals of four species of bush crickets in marginal populations relative to core populations (Simmons & Thomas 2004), increased flight muscle relative to body mass in recently founded populations of *Pararge aegeria* (Lepidoptera) (Hill et al. 1999) and the progressive increase in leg length during invasion of Australia by *Bufo marinus* (Amphibia) (Phillips et al. 2006).

In the case of Odonata, such dispersal traits may include proportionally larger thoraces, i.e. greater flight muscle mass, lower wingloading, higher wing aspect ratio and increased body size. Some of these traits, e.g. wingloading, have been studied in Odonata but analyses have focused on interspecific variation rather than intraspecific variation (Grabow & Ruppell 1995). In addition to increases in the magnitude of dispersal traits, there may be a concurrent decrease in the magnitude of non-dispersal traits reflecting a trade-off based on finite energy resources. Such a trade-off may involve declines in fecundity, e.g. a reduction in abdominal mass leading to a reduction in wingloading, or a decline in immune function.

## EXTINCTION RISK

Although a warm-adapted taxon, local populations of temperate Odonata are certainly at risk from the rate and extent of projected climate change. This risk results from the loss of fundamental niche space due to geographic constriction at northern range margins. Such a pattern is seen in southern populations of *Leucorrhinia dubia*

(Vander Linden), which are restricted to isolated, high altitude sites in the Pyrenees and Alps (Askew 2004). Fortunately most species, including *L. dubia*, have access to northern habitats into which the range can shift – particularly northern Scandinavia and Russia, which will likely see a large increase in species numbers over the coming years.

A further problem with climate change is the indirect effect of temperature on sea level. Many of the most diverse odonate communities persist in low-lying wetlands such as the Fens in England and the wetlands of the Netherlands, which are below sea level. Inundation by sea water of vast areas appears to be almost inevitable given the present rate of sea level rise (Meehl et al. 2005). As mentioned above, flooding has already been implicated in the extinction of *Coenagrion scitulum* from southern England.

One hundred odonate species are listed on the IUCN red list as being either endangered or critically endangered (for a review of IUCN regional reports, see International Journal of Odonatology, vol. 7, issue 2). Only two species are thought to be extinct, both of which are insular: *Megalagrion jugorum* (Perkins) from the Hawaiian Islands and *Sympetrum dilatatum* (Calvert) from the Atlantic island of St Helena (IUCN 2008). This observation and their extensive evolutionary history suggest that Odonata are robust to extinction pressures. However, it must be borne in mind that insect extinctions are difficult to verify (Dunn 2005), even in relatively conspicuous species such as Odonata.

## SUMMARY

The Odonata exhibit a range of adaptations that allow them to respond to variations in temperature. This enables them to persist in fluctuating environments, sometimes spanning a broad range of abiotic conditions. The responses exhibited by Odonata to varying thermal regimes have been detected at a range of scales from the physiological studies of May (1976) through the behavioural experiments of Thompson (1978c) to the macroecological observations of Hickling et al. (2006) and Hassall et al. (2007).

It is likely that future impacts on odonates will largely involve a spatial shift of communities and their associated ecological interactions. However, this relies on the rates of responses of trophic, dispersal and developmental traits being equal among species, a situation which is highly unlikely.

The majority of species are predicted to benefit from the warming through poleward expansions of range. Even in boreal species, climate space often still exists beyond the current geographical distribution. However, a particular threat to odonates comes in the form of habitat fragmentation. Species-specific habitat requirements, pollution and mismanagement of water bodies result in what appears to be a dense network of water bodies being largely unusable for some species. This, coupled with poor dispersal, represents a challenge to the tracking of climate space by certain species.

Much more research is required into the Odonata, not only because they represent an important part of many aquatic communities but also because this taxon's thermal sensitivity makes it a potential barometer for environmental change. Such research should focus on the physiological responses underlying broad-scale patterns of change. Specifically: the identification of range-determining factors through physiological experiments and experiments to investigate the difference in systems with and without vertebrate predators.

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